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CHROMOSOME NUMBERS IN SOME AMERICAN FARINOSE PRIMULAS WITH COMMENTS ON THEIR TAXONOMY[1]

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The genus *Primula* presents interesting cytotaxonomic problems. Comprised of a number of both disputed and confusing species, the genus is a classical example of the utility of chromosome number determinations in elucidating species relationships. Bruun (1930, 1932) in an extensive cytological study of *Primula,* found that the subsection *Eu-Farinosae* is characterized by a basic number of x = 9 and that among its Eurasian species there occurred chromosome levels of 2x, 4x, 6x, 8x, and 14x. A separate subsection, proposed by Bruun (1932) on the basis of its cytological distinctness, includes several species with the basic number of x = 8.

The published data on the cytology of the American farinose primulas are scanty. And this has largely been obscured because reported chromosome number determinations for native species have been merely included in papers in which investigations other than cytological have been emphasized (Bruun, 1938; Thomas, 1951). It is my purpose here to summarize the available information as to chromosome counts for the American farinose species and to report my own cytological findings.

[1] Some of the data reported here are included in a dissertation entitled, "A Biosystematic Study of *Primula mistassinica* Michx.", which was submitted by the author to the University of Michigan in partial fulfillment of the requirements of the Degree of Doctor of Philosophy.

I am indebted to Drs. Doris and Askell Löve of the Botanical Institute of the University of Montreal for providing me with unpublished data. In particular I wish to express my appreciation to Dr. Askell Löve and Dr. Alexander Gershoy of the Botany Department of the University of Vermont for reading the manuscript and offering many helpful suggestions and comments.

SOURCE OF MATERIALS AND METHODS

The plants used for the present study were obtained either from germinated seeds taken from herbarium specimens or from living individuals transplanted to the greenhouse from their native habitat. All specimens were grown at the Botanical Garden of the University of Michigan during the years 1954 and 1955. This provided the opportunity to compare the morphological variations of plants in the greenhouse growing under uniform conditions which helped to interpret variations found in the field. Whenever plants found widely separated geographically, or plants within a particular population at a given site, showed obvious phenotypic differences these were carefully examined cytologically to determine whether correlated karyotypic differences also occurred. Voucher specimens were made of the experimental plants and these, together with the author's field collections are housed in the Pringle Herbarium of the University of Vermont.

Comparatively large collections were made of both *P. mistassinica* Michx. (including *P. intercedens* Fern.) and *P. laurentiana* Fern. Representatives of 16 populations of *P. mistassinica* covering much of its range in eastern North America were studied cytologically. Plants of *P. laurentiana* were also examined from collections taken from 9 stations in the Gaspé Peninsula and in Newfoundland.

Chromosome determinations were made mainly from root tips by use of the acetocarmine squash technique, after preliminary fixation in chloroform-ethanol-acetic acid (4:3:1).

OBSERVATIONS

Primula mistassinica Michx. is a widely distributed species in boreal North America found growing in a variety of calcareous habitats including wet sedgy or mossy sites, stony or marly lake shores, and on shaded wet ledges or faces of cool bluffs. Root tip squashes from all plants investigated had a chromosome number of 2n = 18 (Figs. 1-9). Table 1 shows the localities from which material was obtained. Chromosome numbers were constant regardless of geographical location or differences in habitat. Superficially the chromosomes appeared alike in size and shape in all plants examined.

Pronounced variation in leaf size, shape, and degree of farinosity was observed among the cultivated plants, this being particularly true for representatives from the Great Lakes region. Some individuals could well be assigned to *Primula intercedens* Fern., which Fernald (1928) described as endemic to the upper Great Lakes region. Selected plants showing extremes of all variations were carefully studied in an attempt to detect cytological differences and none was found.

The question of validity of *Primula intercedens* as a good species will be the subject of a forthcoming paper; however it is here advisable to make a few comments about this species in order to clarify its treatment in the present investigation. Fernald (1928) separated *Primula intercedens* from *Primula mistassinica* pointing out that the former had yellow-farinose leaves and calyces, and angulate, truncated, and strongly rugose seeds. According to Fernald, *Primula mistassinica* is generally efarinose with rounded and smooth seeds. Hesitant about the validity of his newly described species he adds (Fernald, 1928, p. 87), "*P. intercedens* is here proposed without full confidence of its specific value; but it seems most likely that, in the upper Great Lake region, where it occurs in the same areas as typical *P. mistassinica*, the two have become much crossed." Other taxonomists have indicated their difficulty in separating the two presumed taxa (Butters & Abbe 1953) and a few chose not to recognize the specific status of *P. intercedens* (Brown, 1937; Gleason, 1952). The present author's investigations based on field and transplanted populations, supplemented by herbarium specimens, fail to substantiate any consistent morphological differences between the two species. Since the present cytological study also fails to reveal karyological differences the present writer includes in the variable *P. mistassinica* complex the plants assigned to *P. intercedens*.

TABLE 1. Chromosome numbers of P. mistassinica

Species	*Locality*	*2n*
P. mistassinica Michx., var. mistassinica f. mistassinica (including P. intercedens Fern.)	MICHIGAN:	
	Cheboygan Co.: Grass Bay (Vogelmann 547 VT).	18
	Presque Isle Co.: Hammond Bay (Vogelmann 548 VT).	18
	Emmet Co.: Little Traverse Bay (Vogelmann 541 VT).	18
	Mackinac Co.: S. Gould City (Vogelmann 545 VT)	18
	Hog Island Creek (Vogelmann 544 VT)	18
	Davenport Creek (Vogelmann 546 VT)	18
	Alger Co.: Pictured Rocks (Vogelmann 549 VT)	18
	Miner's Falls (Vogelmann 533 VT)	18
P. mistassinica var. mistassinica f. leucantha Fern.	QUEBEC:	
	East Gaspé Co.: Percé (Vogelmann 654 VT)	18
	NOVA SCOTIA:	
	Victoria Co.: Cape North Village (Smith, et. al. 3750 MT)	18
	NEWFOUNDLAND:	
	St. Georges Port-Au-Port Distr.: Green Head (Rouleau 3709 MT)	18
	St. Barbe Distr.: Bonne Bay (Rouleau 3334 MT)	18
	Humber Distr.: Serpentine River (Rouleau 1865 MT)	18
	White Lake (Rouleau 2041 MT)	18
P. mistassinica var. noveboracensis Fern.	MICHIGAN:	
	Eaton Co.: Grand Ledge (Vogelmann 617 VT)	18
	NEW YORK:	
	Tompkins Co.: Taughannock Creek (Vogelmann 616 VT)	18

Primula laurentiana Fern., a quite robust species, is found in the Gaspé Peninsula, Newfoundland, and on the north shore of the St. Lawrence River where it usually grows on calcareous slopes or ledges. A list of localities from which specimens of *Primula laurentiana sensu str.* were obtained for chromosome counting is given in Table 2. The eight populations studied, including transplants and plants grown from seeds, were octoploids, 2n = 72 (Fig. 10). Several meiotic figures, obtained from an anther squash of a plant from St. Barbe District, Newfoundland, showed good pairing (Fig. 13).

A single population, collected from "grassy talus slopes" between Chimney Cove and Shoal Point, in the Humber District of western Newfoundland, grown from seeds of plants collected by Dr. Ernest Rouleau (No. 3405), on deposit in the Marie-Victorin Herbarium of the University of Montreal, was found to have 2n = 54 (Fig. 11). Phenotypically these plants fell within the range of variation found in *P. laurentiana;* however, detailed examinations designed to clearly separate the "grassy talus" hexaploids from the groups of octoploids were not made in the present study.

Table 2. Chromosome numbers of P. laurentiana. s. str.

Species	*Locality*	*n*	*2n*
P. laurentiana Fern.	QUEBEC:		
	Rimouski Co.: Rimouski (Raymond and Kucyniak 1673 MT)		72
	West Gaspé Co.: Tourelles (Pere Louis-Marie and R. Cayouette 50183 MT)		72
	NEWFOUNDLAND:		
	St. Barbe Distr.: Bonne Bay (Rouleau 3320 MT)	36	72
	Humber Distr.: s. of Chimney Cove (Rouleau 1374 MT)		72
	n. e. of Serpentine River (Rouleau 1785 MT)		72
	s. w. of Black Head (Rouleau 1612 MT)		72
	Weebald (Rouleau 1576 MT)		72
	Big Island Cove (Rouleau 1300 MT)		72

Primula incana Jones. The widely ranging species, *Primula incana* Jones, is found growing in wet, calcareous, subalpine meadows of the Rocky Mountains. From transplants of *P. incana* collected in a wet meadow near Jefferson, Colorado, a definitive root tip chromosome count of 72 was obtained

(Fig. 14.) The chromosomes of this octoploid species appear slightly smaller than those found in octoploid *P. laurentiana* and decidedly smaller than those of the diploid *P. mistassinica.*

Primula specuicola Rydb. shows an unusual site preference within the arid regions of southeastern Utah and Arizona. Typically it inhabits the moist, shaded walls of shallow caves found in calcareous sandstone cliffs. Plants of this species are quite large, both upper and lower leaf surfaces being densely covered with whitish farina. Cytological studies indicate that it is a diploid.

The differences between the diploid *P. specuicola* and *P. mistassinica* emphasize striking dissimilarities in vegetative and floral structures. However, *P. specuicola* like *P. mistassinica* produces heterostyled flowers, a phenomenon which seems to be common among diploids but not polyploids of this section as stressed by Ernst (1953).

Primula hunnewellii Fern., described by Fernald (1934) from collections made on the limestone cliffs of the North Rim of the Grand Canyon, Coconino Co., Arizona, differed from *P. specuicola* in having a much smaller calyx and an exserted capsule. It is of interest that Kearney and Peebles (1942, p. 666) list it as a questionable synonym of *P. specuicola* stating that the "type of the doubtfully distinct *P. hunnewellii* also from the Grand Canyon". The present author's observations tend to support this interpretation since he found both exserted and included capsules among a number of plants from a single population near Bluff City, Utah (type locality for *P. specuicola*). The size of the calyces among these plants was variable, none being found as small as Fernald recorded for *P. hunnewellii.*

A summary of the known chromosome numbers in the North American farinose primulas is given in Table 3. Ernst (1953) has presented a chart showing the "ploid" levels for seven American species of the subsection *Eu-Farinosae* in which the Alaskan *Primula borealis* is given as a diploid, and *P. incana* is indicated as an octoploid. Bruun's cytological work is cited by Ernst as the basis for his list. Regrettably it is not clear to the present author whether the "n" counts which Bruun (1938, p. 252) gives in parentheses after *P. mistassinica* and *P. laurentiana* are also intended to apply to those species which precede them in his listing.

TABLE 3. Chromosome numbers of some North American primulas in the subsection Eu-Farinosae

Species	*n*	*2n*	*Reported by*
P. borealis Duby		18	Thomas (1951)
P. incana Jones		72	Vogelmann
P. laurentiana Fern. s. lat.	36		Brunn (1938), Vogelmann
		72	Vogelmann
		54	Vogelmann
P. mistassinica Michx.	9		Bruun (1938)
var. mistassinica f. mistassinica (incl. P. intercedens Fern.)		18	Vogelmann
var. mistassinica f. leucantha Fern.		18	Vogelmann
var. noveboracensis Fern.		18	Vogelmann
P. specuicola Rydb.		18	Vogelmann
P. stricta Hornem. (det. on Swedish and Icelandic plants and from Churchill, Manitoba)		126	Bruun (1930, 1932) Löve and Löve (1956 and unpublished)

DISCUSSION

The widespread native diploid species, *P. mistassinica,* is considered here to be the North American counterpart of the widespread Eurasian diploid *P. farinosa.* This idea is given support not only by the chromosome number common to both species but also by the close phenotypic similarity to *P. farinosa* which exists among some of the plants in the variable *P. mistassinica* complex. Generally, plants of *P. mistassinica* are slender and efarinose yet some individuals, particularly those growing on calcareous sandstone ledges in the Great Lakes region, are difficult if not impossible to distinguish from certain plants of *P. farinosa.* Hybridization studies are needed to establish indices of crossability and fertility.

Where the northwestern range of *P. mistassinica* ends, the range of *P. borealis* begins (see maps in Hultén 1948, p. 1336). This Alaska and Yukon species has also proven to be diploid (Thomas, 1951). Even if these species are not conspecific they are certainly closely related as is evidenced by phenotypic characters found in common and by chromosome morphology.

Phenotypic similarities between the octoploids *P. laurentiana* and *P. incana* have already been recognized (Hultén, 1948; Fernald, 1928). *P. scandinavica* of Europe, also an octoploid species, may well be a near relative of our North American taxa. Such herbarium specimens as have been available indicate similarities to *P. laurentiana*.

Still another octoploid, *P. decipiens,* grows in the southern cordillera in South America (Bruun, 1930, 1932). This species bears more similarity to *P. incana* of the Rocky Mountains than any other species, a fact noted by Fernald (1928, p. 74) who stated: "In its subcapitate inflorescence and plane bracts *P. incana* is nearer related to *P. decipiens* of southern South America (*P. magellanica* of authors) than to other members of the *Farinosae*". Bruun (1932) also points out that the chromosomes of the octoploid *P. decipiens* are three-fourths as long as *P. farinosa* which ratio is similar to the size relationship obtained by this writer in a comparison of *P. incana* and *P. mistassinica*. The smaller chromosome size of both *P. incana* and *P. decipiens* may be a further indication that both species differentiated from a common ancestral stock.

Although the diploids are widespread in Eurasia and North America, it appears that the octoploids and the tetrakaidekaploid (14-ploid) *P. stricta* have been most successful in establishing themselves throughout arctic and mountainous regions generally regarded as having severe environments (Stern 1949). The widespread recurrence of octoploid species, as for example *P. capitellata* in the alpine areas of southern Persia, *P. scandinavica* in Scandinavia,

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New York (8) 1455X and Grand Ledge, Michigan (9) 970X. FIG. 10. 72 chromosomes of *P. laurentiana* from Bonne Bay, Newfoundland. 1455X. FIG. 11. 54 chromosomes of *P. laurentiana* from between Shoal Point and Chimney Cove, Newfoundland. 1455X. FIG. 12. *P. specuicola* from near Bluff City, Utah. 970X. FIG. 13. 36 bivalents from pollen mother cells of *P. laurentiana* from Bonne Bay, Newfoundland. 970X. FIG. 14. 72 chromosomes of *P. incana* from Jefferson, Colorado. 970X. FIG. 15. *P. borealis*, 2n = 18, drawn from a root tip cross-section prepared by Dr. Henry J. Thompson and provided for publication by Dr. John H. Thomas.

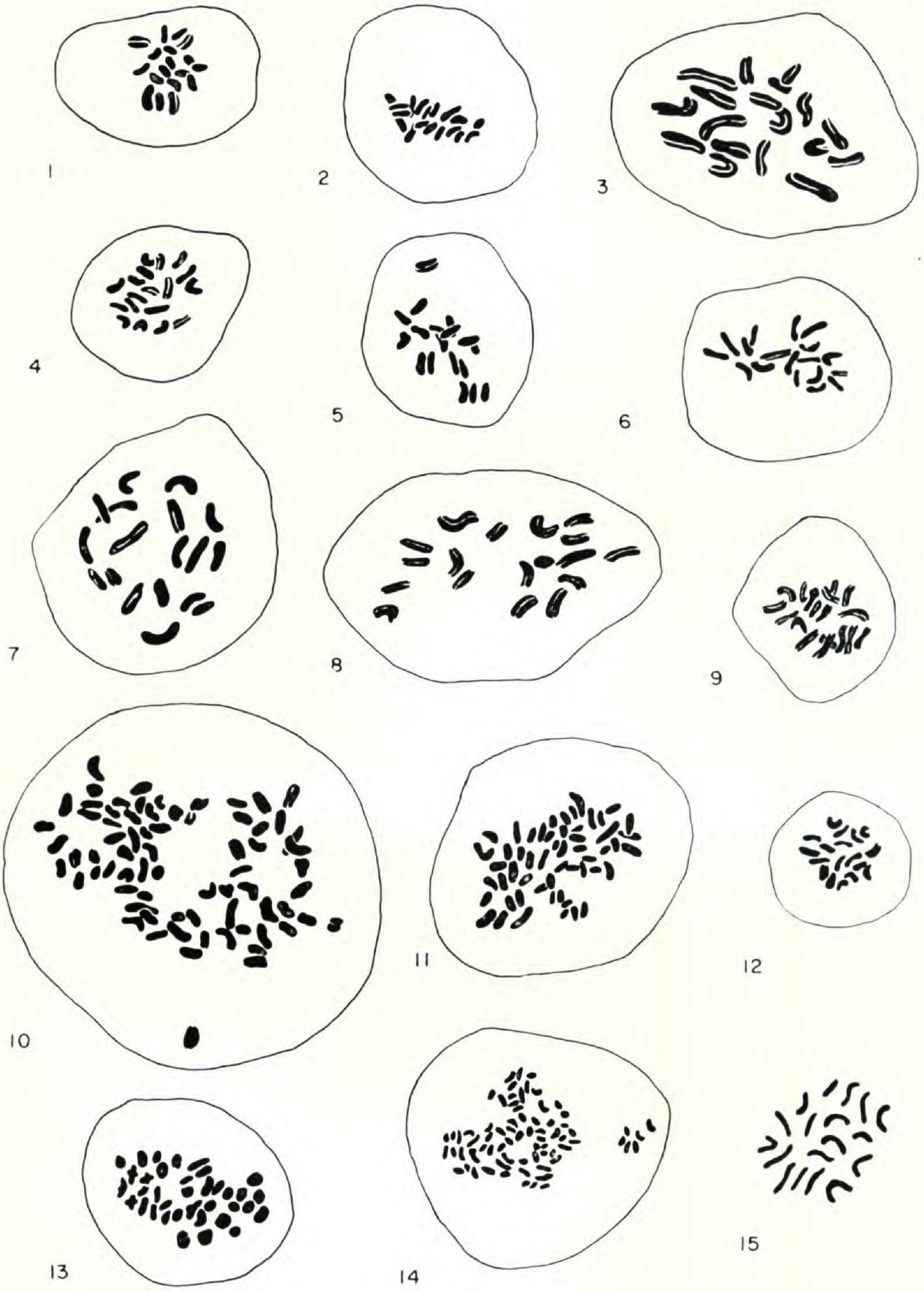

FIG. 1-14. Chromosomes of several North American primulas of the subsection *Eu-Farinosae*. All figures show root tip chromosomes at somatic metaphase unless otherwise indicated. FIG. 1. *P. mistassinica* from Grass Bay, Michigan. 1455X. FIG. 2. Chromosomes of an exceptionally large plant of *P. mistassinica* from Grass Bay, Michigan. 970X. FIG. 3-6. *P. mistassinica* f. *leucantha* from Newfoundland: Bonne Bay (3) 1455X; Serpentine River (4) 1455X; White Lake (5) 970X; Green Head (6) 1455X. FIG. 7. *P. mistassinica* f. *leucantha* from Cape North Village, Nova Scotia. 1455X. FIG. 8-9. *P. mistassinica* var. *noveboracensis* from Taughannock Creek,

P. laurentiana in Laborador, Nova Scotia, and the Gaspé, *P. incana* in the Rocky Mountains, and *P. decipiens* in the southern Andes, Cape Horn, and the Falkland Islands, may well be an indication of a very old and formerly highly successful complex. The present day discontinuous distribution of these species may, perhaps, indicate fragmentation of a formerly very wide-ranging species by Pleistocene glaciations.

The presence of a hexaploid plant in collections of *P. laurentiana,* sensu lat., in Newfoundland indicates that additional cytological studies are needed to determine whether this chromosome number, unique for this species, is of local or more widespread occurrence and whether there are morphological or ecological characteristics associated with it. When Bruun's (1930, 1932) investigation of the *Farinosae* revealed that the octoploid *P. scandinavica* (then called *P. scotica* var. *scandinavica*) was cytologically and geographically distinct from *P. scotica* (cf. also Dovaston, 1955), he observed dissimilarities in the leaves, scapes and stigmas (Bruun 1938). It should be noted that Smith and Fletcher (1943) are not convinced of the leaf and scape criteria used by Bruun although they do accept the validity of the species.

The relation of *P. specuicola* to other members of the farinose group is not clear. Since it is a diploid ($2n = 18$), and thereby holds a basic phyletic position, its taxonomic position deserves further investigation. The species does not appear to be closely related to any other American taxa. Rydberg (1913) suggests that it is near *P. farinosa* and *P. incana* and Fernald (1928, p. 86) states that "*P. specuicola* may be nearer related to *P. rusbyi* Greene ($2n = 44$, Bruun 1932) than to the *Farinosae*". The abundance of farina on the leaves and flowers of *P. specuicola,* combined with the fact that its basic chromosome number of 9, seems to fix the position of this species with the *Eu-Farinosae* complex.

P. specuicola is quite distinct from other species of the section in its ecological preference. Growing on moist calcareous sandstone walls of shallow caves in the arid regions of southwestern United States its habitat displays a striking contrast to that within which most members of the *Farinosae* are found. The latter are usually found at much higher latitudes and/or altitudes where the macroclimate is considerably cooler and moist. Unquestionably *P. specuicola* is subjected to severe environmental fluctuations such as high temperatures and, perhaps, occasional periods of dryness.

The circumpolar and arctic species, *P. stricta* Hornem., has the highest number reported for the genus, or 2n = 126 chromosomes. This 14-ploid complement has been determined by Bruun (1932) on plants from two localities in Sweden and by Löve and Löve (1956) on material from northern and eastern Iceland. Populations from Churchill in Manitoba, collected and fixed by Dr. J. C. Ritchie of Winnipeg, were found to have the same high chromosome number (Löve and Löve, unpubl.) Thus there are good indications that this high chromosome level is maintained throughout its extensive arctic distribution.

The tendency toward polyploidy well-established among Eurasian species in primulas of the subsection *Eu-Farinosae*, is also revealed in the North American taxa. Thus chromosome levels of 2x, 6x, 8x, and 14x have been found within American species. In view of such data some revision is needed in the map of distribution of "ploid" levels in the *Eu-Farinosae* by Stern (1949), later used by Darlington 1956). The widespread occurrence of diploid and polyploid species in both hemispheres needs to be given serious consideration when evaluating the evolutionary development of the *Eu-Farinosae* complex. Of more general interest, the geographical patterns of "ploid" levels illustrated by this group may contribute to a better understanding of the history and distribution of the circumboreal flora. — UNIVERSITY OF VERMONT.

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